

TAXONOMIC STUDIES IN FREZIERA (THEACEAE),  
WITH NOTES ON REPRODUCTIVE BIOLOGY

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Three new species of *Freziera*, one each from Venezuela (from the Guayana Highland), Colombia, and Ecuador (both from the Andes), are described, illustrated, and compared to related species. The monotypic genus *Patascoya* is reduced to synonymy in *Freziera*, and the appropriate combination is made. Observations of herbarium specimens and natural populations suggest an unequal sex ratio in this dioecious genus, with carpellate plants predominating. This is the reverse of the situation in most tropical forest trees.

*Freziera* Willd. is a Neotropical genus of trees mostly distributed in cloud forests in northwestern South America. It is easily recognized by its alternate, distichous leaves and its axillary clusters of flowers. Most species grow at high altitudes, close to the upper limit of cloud forests. A few species grow at lower altitudes in moist coastal regions in Colombia, Panama, and Venezuela.

Species of *Freziera* are trees 5 to 15 (to 35) m tall, or rarely shrubs. The leaves of all species are alternate and distichous. Flowers are axillary and solitary or in racemose fascicles of two to seven (to 15). The pedicel of each flower is subtended by a single bract (or by two bractlike structures in some species with exclusively solitary flowers). As in most Theaceae, each flower has two bracteoles; in *Freziera* they are nearly always apical on the pedicel and often appear to be part of the calyx, since they are attached to the floral receptacle and may be quite sepaloid in appearance (FIGURES 1c, 2d). The corolla of all species of *Freziera* is urceolate and thickened above. The thickening is made up of sclereids, although in the field the corolla looks and feels quite waxy. The petals spread only at the tips, and the opening is, as far as I have observed, 1 mm or less in diameter. The stamens and stigma are well within the flowers. The pollen grains of *Freziera* are small, averaging ca. 10  $\mu\text{m}$  in diameter, and copious. The fruits are berries, which are nearly always immature on herbarium specimens. Although carpellate plants usually have everything from buds to large green fruits, I did not find mature fruits (reportedly blue or black) in the field. Seeds from the largest green fruits fail to germinate, implying that they are immature.

Species of *Freziera* occur in cloud and moist coastal forests at elevations up to 3500 m, and the genus is distributed in the West Indies (Cuba, Jamaica, and the Lesser Antilles), southern Mexico, Central America, and much of South

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America (the Guayana Highland, the Venezuelan coastal cordillera, and the Andes south to central Bolivia).

Morphologically, *Freziera* has gynodioecious flowers; however, all species for which there are sufficient data are functionally dioecious. Carpellate plants have flowers with staminodia and a functional gynoecium. The flowers in staminate plants have functional stamens and usually have what appears to be a functional gynoecium but nearly always fall off soon after anthesis. Only three collections of one species (*F. chrysophylla* Bonpl.) have so far been observed to be hermaphroditic. These specimens have flowers with nearly 100 percent viable pollen (tested with cotton blue in lactophenol) on the same branch as fruits. The flowers may be truly hermaphroditic, or the flower type may have changed as the branch matured.

In herbaria there are far more specimens of *Freziera* representing carpellate plants than staminate ones. Of 448 collections of about 29 species, 303 (67.6%) are carpellate, 102 (22.8%) are staminate, and 43 (9.6%) either are sterile or have buds too young for determination if anthers would develop or not. In 86 specimens of *Freziera candicans* Tul., the ratio is 62:20:4 (72.1:23.3:4.6 percent), respectively, and in 49 of *Freziera canescens* Bonpl., 40:5:4 (81.6:10.2:8.2 percent). This unequal sex ratio in collections may be due to collection artifact or to unequal sex ratios in natural populations. I suspect that one reason for the preponderance of carpellate specimens may be that botanists, in trying to collect what appear to be better specimens, select those with buds, flowers, and fruits (i.e., specimens from carpellate plants), rather than ones with only buds and flowers. Since staminate and carpellate flowers are externally identical, many collectors probably do not realize the importance of separate collections of the two sexes.

There may be a truly unequal sex ratio in *Freziera*. It is usually harder to find staminate than carpellate individuals in the field; in some small populations (about eight to ten observed individuals) I was unable to find any staminate plants at all. According to Opler and Bawa (1978, and references therein), dioecy is more common in tropical ecosystems than in temperate ones (see also Bawa, 1980), and dioecious plants often have sex ratios that depart from unity. Forty-four percent of the dioecious tropical forest trees they studied had sex ratios departing significantly from unity: of ten species, eight were biased toward a greater number of staminate individuals, and only two were carpellate-dominant (both were members of the Polygonaceae, a family known for carpellate-dominant sex ratios (Opler & Bawa, 1978)). Lloyd (1973) found that when sex ratios are skewed, perennials tend to show an excess of staminate plants, the reverse of the apparent situation in *Freziera*.

Explanations advanced for carpellate-dominant sex ratios in plants include differential survival rates, differential reproductive maturation, and seral position (Opler & Bawa, 1978). Further field study of *Freziera* is necessary since my observations of individual sex ratios are anecdotal rather than quantitative. If the genus is really carpellate-dominant in natural populations, it is very unusual among tropical trees.

The three new species and one new combination proposed below result from work on a monograph of the entire genus.

**Freziera carinata** A. Weitzman, sp. nov.

FIGURE 1.

A speciebus aliis Frezierae in ramulis alatis, foliis auriculis basalibus demum revolutibus (foliis ut videtur base abrupte attenuatis), et costis petiolis carinatis, differt.

Small tree 2–9 m tall; mature branches terete; twigs dorsoventrally flattened, with narrow paired wings decurrent from base of petiole keel and descending through 2 internodes; bark dark red-brown, papillate when young, striate and splitting with age, glabrous or occasionally very short-strigose-glabrescent; lenticels few, large, very narrowly to widely elliptic, appearing late; terminal bud conduplicate-involute, (2–)4–6.3 cm long, finely strigose. Leaves with petiole (0.1–)0.3–0.6(–1.8) cm long, erectly winged, canaliculate above, keeled below, glabrous; colleter(s) 1 to several in petiole base, linear or triangular, flattened, red to black; blade elliptic or narrowly obovate, (4.1–)9.2–14.8 by (2.1–)2.9–4.9(–6) cm, coriaceous, the base rounded, ciliolate, auriculate, with auricles becoming revolute (base then appearing attenuate), the apex acute, short-acuminate, ultimately retuse, terminating in caducous, thick, conical, black seta, the margin finely serrate, teeth (46 to) 71 to 95 (to 122) per side, with caducous, thick, conical or slightly curved, forward-pointing, black setae inserted in the sinuses (rarely—only in specimens from Cerro de la Neblina—with few thin hairs surrounding base of each seta), the surface glabrous above, densely short-strigose (rarely glabrous) below, with small papillae densely and evenly distributed above and below, and larger ones on midrib in horizontal rows above and scattered below, the midrib flat with small central ridge above, keeled below, the lateral veins (16 or) 17 to 24 (to 31) per side, flat to slightly rounded above, prominently rounded below. Inflorescence axis 0.5–2.5 mm long, with flowers 1 to 5, pedicel scars absent or 1 to 5 and contiguous; floral bract persistent, triangular, 1.1–3.1 by 0.8–1.5 mm, sclerotic, the base clasping, the apex acute to rounded, terminating in thick, conical, black seta, the margin entire, sometimes with several black setae and/or flaps, sometimes ciliolate, the outer surface sparsely to densely sericeous; pedicel erect, cylindrical, 3.1–6 by 0.7–1.1 mm, glabrous to strigose; bracteoles 2, apical on pedicel, subopposite, persistent, sepaloid, seemingly part of calyx, broadly to very broadly ovate, equal or unequal, 1.4–2.4 by 1.5–2.4 mm (lower), 1.8–3 by 1.9–2.9 mm (upper), sclerotic basally and chartaceous above, the base clasping or cordate, the apex rounded, with terminal or subterminal (on outer surface) thick, conical, black seta on lower (or rarely both) bracteole(s), the margin ciliolate, with basal conical, dark setae, the outer surface sparsely strigose or centrally glabrescent. Flowers 4.7–7 by 3.1–4.1 mm; sepals 5, broadly ovate, nearly equal, 2.2–3.8 by 2.1–3.1 mm, sclerotic basally and chartaceous above, the base cordate, the apex rounded and often splitting, the margin membranaceous, minutely ciliolate, with dark or pale basal flaps, the outer surface glabrous to minutely strigose, the inner surface glabrous; corolla urceolate, the petals 5, slightly connate basally, ovate, nearly equal, 3–5.8 by 1.5–2.5 mm, membranaceous in lower  $\frac{1}{3}$ , sclerotic above, apically acute, recurved at anthesis. Staminate flowers with stamens (14 or) 15, uniseriate, free or slightly adnate basally, unequal, unordered, the filaments unequal, flat, linear, ca. 0.9 and ca. 1.4 mm

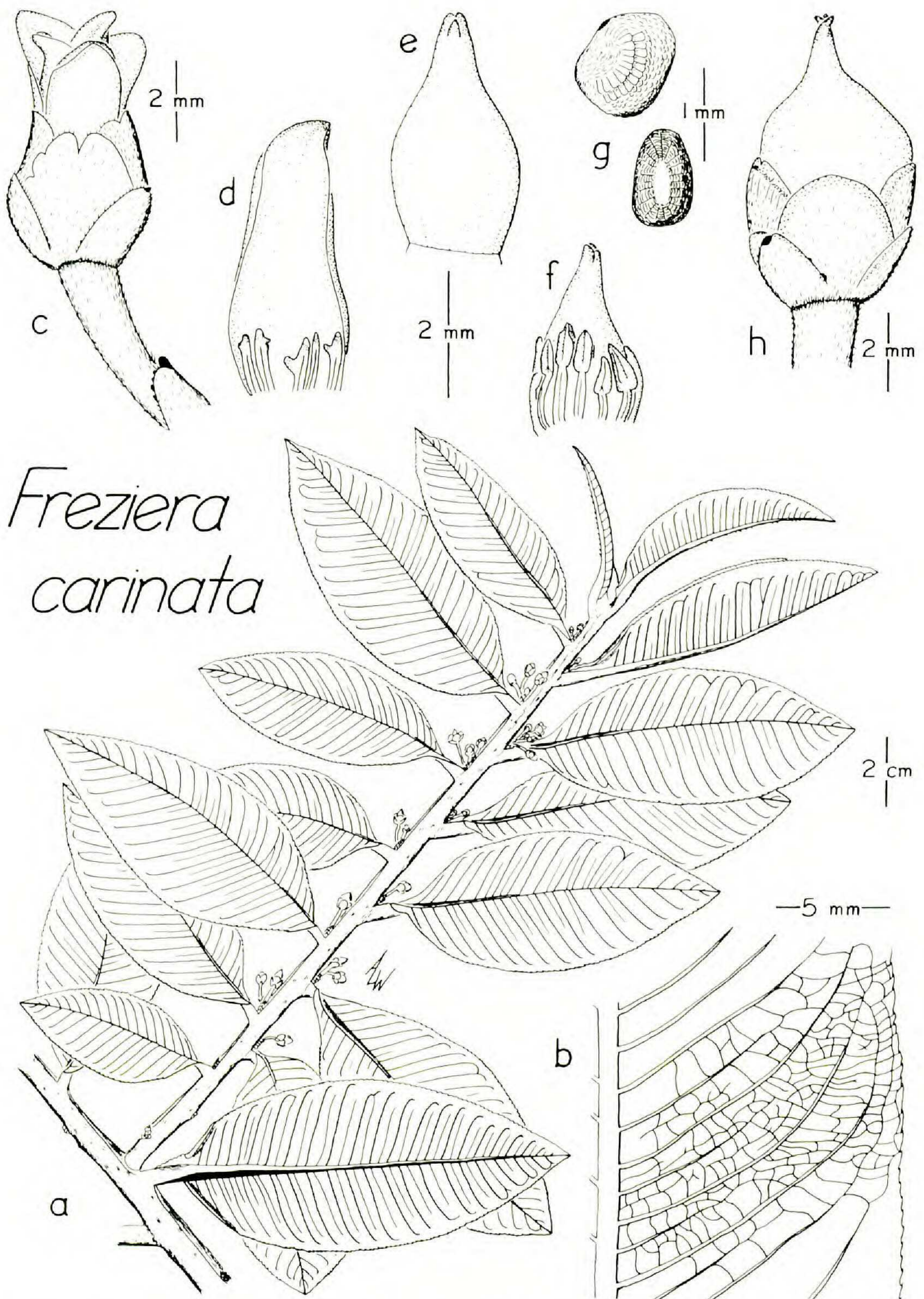


FIGURE 1. *Freziera carinata*: a, habit; b, undersurface of leaf; c, flower; d, petal of carpellate flower, stamens adnate; e, gynoecium of carpellate flower; f, ovary and stamens of staminate flower; g, seeds, side and chalazal views; h, fruit (b, f from holotype; c-e, g, h from Maguire & Maguire 35334).

long, the anthers linear, equal, 0.8–0.9 mm long, lightly pigmented, basally cordate, the apiculus ovate, ca. 0.1 mm long, apically rounded; gynoecium conical, 2.4–3.2 by 1.5–1.7 mm, the ovary 3-locular, with locules ca. 1.5 mm long, each containing ca. 12 ovules, the style tapering, the stigmatic lobes 3, erect, 0.25–0.35 mm long, dark, minutely papillate. Carpellate flowers with staminodes 15 (or 16), uniseriate, free, linear, flat and rarely with peripheral flaps, equal or unequal, 0.6–1.6 mm long, apically rounded; gynoecium conical, 3.2–4.9 by 1.7–2.1 mm; the ovary (2- or) 3-locular, with locules 1.3–1.8 mm long, each containing 16 to 30 ovules, the style tapering, the stigmatic lobes (2 or) 3, erect, 0.2–0.3 mm long, dark and minutely papillate. Immature fruits globose, tapering abruptly into persistent style, 6.9–7.7 by 4.9–5.7 mm, green; mature fruits unknown but reportedly blue; immature seeds (6 to) 16 to 29 per locule, reniform, 1.2–1.4 mm long, dark red, the testa reticulate.

TYPE. Venezuela, Edo. Bolívar, Auyan-tepuí, cumbre de la parte central occidental (división occidental del cerro), vecindad del "Drizzly Camp," sobre piedra de arenisca, a lo largo de afluente del Río Churún, 1760 m, 4 May 1964, *J. Steyermark 93366* (bud, ♂ fl<sup>2</sup>—holotype, GH; isotypes, NY, U (n.v.), US, VEN).

ADDITIONAL SPECIMENS EXAMINED. **Venezuela.** TERR. FED. AMAZONAS: Serranía Yutajé, Cerro Yutajé, Río Manapiare, 2100 m, *Maguire & Maguire 35334* (♀ fl, fr; NY (3 sheets)); Cerro de la Neblina, Río Yatúa, NW head of Cañón Grande, 2000 m, *Maguire et al. 42322* (young fr; NY); Cerro de la Neblina, limite Venezuela-Brasil, altiplano, 1800–2000 m, *Ewel 177* (bud, young fr; MY, NY); Cerro de la Neblina, Camp VII, 5.1 km NE of Pico Phelps, 1730–1850 m, *Nee 30641* (mixed coll., bud, ♂ & ♀ fl, fr; liquid-preserved material GH, duplicates yet to be distributed); Dpto. Atabapo, below Salto Los Monos on tributary of headwaters of Río Iguapo, 3°35'N, 65°23'W, 1500–1600 m, *Liesner 18515* (bud, fruit; GH); Dpto. Atabapo, gallery forest and open area on Plateau of Huachamacari, 3°50'N, 65°25'W, 1720 m, *Liesner 18073* (bud; GH). EDO. BOLÍVAR: Disto. Cedeño, Serranía Guanay, sector NW, en las cabeceras mas orientales del Río Paraguaza, 5°55'N, 66°23'W, ca. 1700 m, *Huber 11003* (♀ bud, fl, fr; NY); Meseta de Jaua, Cerro Sarisariñama, cumbre, porción NE, interior de la Sima Mayor, 4°41'N, 64°13'W, 700 m, *Brewer-Carías s.n.* (♂ bud; VEN); Cerro Guaiquinima, cumbre, sector NE, cerca del borde, cabeceras de brazo NE del Río Carapo, 5°59'N, 63°25'W, 1490–1500 m, *Steyermark et al. 117329* (♂ bud; MO, NY, U, VEN); Auyan-tepuí, no further locality or date, *Pannier & Schwabe s.n.* (♀ bud, young fr; VEN); Auyan-tepuí, Valle Encanto, lado derecho del Salto Angel, *Foldats 7135* (bud; VEN); Auyan-tepuí, plateau, central E section of NW arm, 5°56'N, 62°34'W, 1850 m, *Prance & Huber 28302* (bud, ♀ fl, fr; GH); Chimantá Massif, SE-facing upper shoulder of Apácará-tepuí, below summit, 2000–2100 m, *Steyermark 75782* (♀ bud, fr; MO, NY, VEN (2 sheets)); Chimantá Massif, central section, along W branch of headwaters of Río Tirica above upper falls, 2090 m, *Steyermark & Wurdack 880* (bud; F, VEN (2 sheets)); Chimantá Massif, altiplanicie en los farallones superiores de Apacará-tepuí, sector N del Macizo, 5°12'N, 62°12' W, ca. 2200 m, *Steyermark et al. 128337* (fr; GH, MO (2 sheets), VEN); Chimantá Massif, sector SE, amplia altiplanicie en la sección NE del Acopán-tepuí, en las cabeceras del Río Yunek, 5°12'N, 62°5'W, 1950 m, *Huber et al. 10118* (bud, ♂ fl; NY); Ptari-tepuí, along base of E-facing high sandstone bluffs, 2410–2450 m, *Steyermark 59937* (bud; A, F); Cerro Venamo (parte SW), cerca de los límites con la Guayana Inglesa, a lo largo del afluente W subiendo el Río Venamo, 950–1150 m, *Steyermark et al. 92345* (bud, ♀ fl, fr; GH, K, US, VEN); Cerro Roraima, no further locality, 2000 m, *Ule 8726* (bud, ♀ fl; K); Cerro Roraima, forested SW-facing quebrada

<sup>2</sup>In the specimen citations below, I state flowering condition and sex for the flower stage observed; if no sex is indicated, floral material was insufficient for examination.

near Rondón Camp, 2040–2130 m, *Steyermark* 58697 (bud, ♀ fl, young fr; A, F); Cerro Roraima, trail through cloud forest to summit, 5°12'N, 60°40'W, 2280–2600 m, *Luteyn & Aymard* 9767 (bud, ♀ fl, fr; GH, NY, U, VEN), 9772 (CAS, GH, NY, VEN).

*Freziera carinata* is characterized by its winged stems and its prominently keeled petioles and midribs. The leaf blades are auriculate, but the auricles become revolute very early and the blades then appear attenuate. Specimens of *F. carinata* are unusual: the young growth of most other species dries dark or light brown or rarely green, while that of *F. carinata* usually dries orange-brown with paler orange spots. Like most species of *Freziera* for which phenology is known, *F. carinata* flowers throughout the year.

Kobuski (1941), who recognized only one species from the Guayana Highland, apparently did not see any specimens of *Freziera carinata* for his monograph of the genus. However, despite having seen only a photo and a leaf fragment of the type of *F. roraimensis* Tul. and no material of *F. guianensis* Klotzsch ex Wawra, he correctly placed the latter in synonymy under *F. roraimensis*, stating (p. 490), “*F. roraimensis* and *F. guianensis* were collected at the same locality by the same collector. There is no doubt in my mind that only one good species exists in this locality. . . .” Although the name *Freziera roraimensis* has been used by Kobuski and subsequent workers in all determinations of Guayana Highland material, that species has not been re-collected since Schomburgk found it in November 1842 in the vicinity of Mt. Roraima. All other known material from the Guayana Highland belongs to *F. carinata*. *Freziera carinata* has been collected on most of the larger tepuis so far visited except Duida. The two species now recognized from the Guayana Highland region can be distinguished by use of the following key:

- Twigs flattened; midribs and petioles strongly keeled; twigs and leaves glabrous to minutely strigose; leaf blades elliptic or narrowly obovate, (4.1–)9.2–14.8 by (2.1–)2.9–4.9(–6) cm; flowers 4.7–7 by 3.1–4.1 mm. . . . . *F. carinata*.  
 Twigs terete; midribs and petioles rounded; twigs and leaves densely long-sericeous and short-villous, leaf blades narrowly elliptic, 8.1–9.7 by 2.6–3.6 cm; flowers 4.4–5 by 2.4–2.7 mm. . . . . *F. roraimensis*.

***Freziera echinata*** A. Weitzman, sp. nov.

FIGURE 2.

A speciebus aliis *Frezierae* in ramulis et foliis utrinque pilis erectis densis longis persistentibus praeditis, setis erectis pilis erectis cingentibus in marginibus foliis instructis, et bracteolis sepalisque dense longe sericeis extus paginis totis et intus versus apices acutes, differt.

Tree ca. 5 m tall; mature branches and twigs terete, dark red-brown, papillate, conspicuously ridged below each side of leaf base, finely striate elsewhere, very densely golden-hirsute, the hairs persistent, erect, of 2 lengths (ca. 3 and 0.5 mm), the lenticels ovate, 0.4–0.6 mm across, splitting vertically; terminal bud conduplicate-involute, 4–6 cm long, erect-hirsute. Leaves with petiole 2–3 mm long, erectly winged, canaliculate, hirsute above and below; blade narrowly ovate, 10.4–12.3 by 2.6–3.5 cm, subcoriaceous, the base unequal with sides asymmetric, truncate or rounded on long side, cuneate to truncate and revolute on short side, the apex long-acute, terminating in caducous, thick, conical,

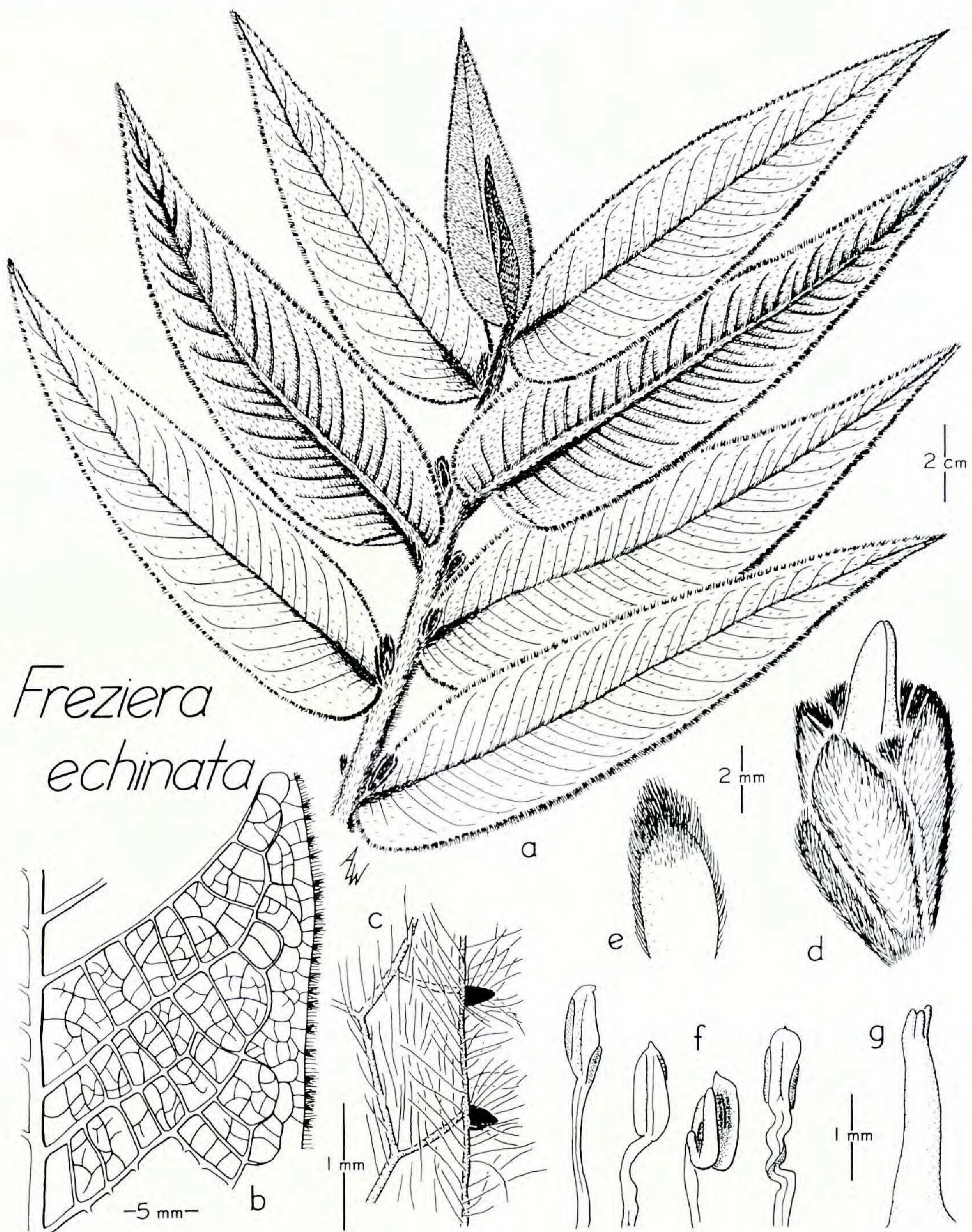


FIGURE 2. *Freziera echinata*: a, habit; b, leaf undersurface (hairs omitted); c, leaf margin; d, flower; e, inside of outer sepal; f, stamens; g, style and stigma (from type).

black seta, the margin entire, slightly revolute, with numerous erect, articulated, conical, black setae ringed by longer erect hairs, the upper surface sparsely hirsute (densely so on midrib) and densely papillate, with hairs persistent, erect, up to 3 mm long, the lower surface densely hirsute, the midrib sunken above, prominently rounded below, the lateral veins 11 to 13 per side, inconspicuous, slightly sunken above, prominently rounded below. Inflorescence axis less than 1 mm long, with 3 to 5 flowers; floral bract persistent, ovate, 6.2–9.3 by 2.1–3.3 mm, sclerotic, keeled, the base clasping, the apex acute, terminating in

thick, conical, black seta, the margins entire, the surface densely long-tomentose; pedicel erect, angled, ca. 1 by 1 mm, densely long-tomentose; bracteoles 2, persistent, sepaloid, ovate, nearly equal, 5–6.4 by 2.6–3.3 mm, sclerotic, the base clasping, the apex acute, the surface densely tomentose outside, tomentose near upper margin inside. Staminate flowers 8.5–9.6 by 5–5.5 mm; sepals 5, ovate, unequal, 6–6.8 by ca. 2.9 mm (outer), 4–5.6 by 2–2.7 mm (inner), sclerotic, the base clasping, sometimes with dark lobes or few dark basal setae, the apex acute, the margin ciliolate, the surface densely tomentose outside, tomentose on upper  $\frac{1}{3}$  (outer sepals) or glabrous (inner ones) inside; corolla urceolate, white, the petals 5, distinct, narrowly ovate, unequal, 6–7.7 by 2.2–2.5 mm (outer), 5.5–6 by 1.6–1.7 mm (inner), membranaceous in lower  $\frac{1}{4}$ – $\frac{1}{3}$ , sclerotic above, apically acuminate; stamens 15, uniseriate, free or slightly adnate at very base, the filaments unequal, geniculate or linear, 1.1–2.2 mm long, flattened at base, cylindrical above, the anthers 1.1–1.2 mm long, connective pigmented, the apiculus 0.05–0.13 mm long, apically rounded and with terminal seta; gynoecium narrowly conical, 3.8–4.9 by ca. 1 mm, the ovary 3-locular, with locules ca. 1.1 mm long, each containing ca. 60 ovules, the style 1.8–2.1 mm long, the stigmatic lobes 3, erect, 0.4–0.7 mm long, dark, minutely papillate. Carpellate flowers and fruits unknown.

TYPE. Colombia, Dpto. Cauca, Parque Nacional Munchique, km 50–55 along road above Uribe, 2256–1875 m, 25 April 1979, *J. L. Luteyn, M. Lebrón-Luteyn, & G. Morales L. 7448* (bud, ♂ fl—holotype, NY; isotypes, AAU, CAS, COL (n.v.), GH, MO).

*Freziera echinata* is characterized by long, narrow leaf blades; long, erect, persistent hairs on both leaf surfaces and on the stems; and erect setae surrounded by erect hairs on the leaf margins. The flowers have densely long-sericeous bracts, bracteoles, and sepals that are conspicuously pointed at the apex. The bracteoles and outer sepals are sericeous inside, a condition unknown elsewhere in the genus. The hairs are so dense that the floral parts cannot easily be distinguished from each other. I have not seen a flower past anthesis, but the most developed buds have extremely long, narrow corollas and petals. Some floral characters are only partly known since the few flowers observed have all been at least partially eaten wherever the sclereids in the tissues are not dense, so the stamens, the base of the petals, and the ovary are usually gone.

This species, known only from the type collection, cannot be confused with any other. No other taxon has this erect pubescence on the twigs and leaves, or the extremely dense, long indumentum on the flowers. *Freziera chrysophylla*, which has similarly shaped leaves, differs from *F. echinata* in having leaves glabrous above and densely golden sericeous below, and pedicellate flowers with round, sericeous bracteoles and sepals. *Freziera tomentosa* Ruiz & Pavón, which like *F. echinata* has sessile flowers, is actually more similar to *F. chrysophylla*, with leaf blades glabrous above and densely sericeous below, but has leaf blades wider than *F. echinata* or *F. chrysophylla* and rounded, glabrous bracteoles and sepals.



*Freziera minima* A. Weitzman, sp. nov.

FIGURE 3a-i.

A speciebus aliis Frezierae praeter *F. stuebelii* (Hieron.) A. Weitzman in habitus fruticoso foliis minutis crenatis, et a *F. stuebelii* in foliis reticulato-venosis differt.

Compact shrub 1 m tall; mature branches terete, brown, the bark conspicuously striate, splitting vertically; twigs square, slightly winged, persistently brown-sericeous, the lenticels large, round, 1–1.7 mm in diameter on older branches, splitting horizontally and vertically; terminal bud merely conduplicate, 1.5–4 mm long, short-sericeous. Leaves with petiole 0.9–3.1 mm long, with narrow, involute wings, canaliculate, sericeous above and below; blade broadly ovate, 7–12.1 by 4.9–10.6 mm, subcoriaceous, the base equal to subequal, obtuse, truncate, round, or slightly cordate, the apex acute or obtuse, ultimately retuse, terminating in caducous, thick, conical, red to black seta, the margin crenate, with teeth 9 to 16 per side, and caducous, thick, conical, short, black setae inserted in the sinuses, the surfaces glabrous, but with few caducous, short, sericeous hairs on midrib above and below, the midrib flat to prominent above, prominently rounded below, the lateral veins 5 to 7 per side, prominently rounded above and below. Flowers solitary, subtended by 2 bractlike structures, these basal on pedicel, persistent, narrowly ovate, 1.5–2.5 by 0.7–0.8 mm, sclerotic, keeled, the base clasping, the apex acute, terminating in thick, conical, black seta, the margin entire, with erect, thick, conical, black setae, the outer surface sparsely short-sericeous; pedicel erect in bud and fruit, recurved at anthesis, cylindrical, 2–2.9 by 0.7–1 mm, ridged, strigose, bracteoles 2, apical on pedicel, opposite, persistent, broadly ovate, unequal, 2.5–2.8 by 1.9–2.5 mm (larger), 2–2.1 by 1.6–1.8 mm (smaller), smaller one sometimes keeled, the base rounded, the apex obtuse to rounded, on smaller bracteole always and on larger one sometimes terminating in conical, black seta, the margin membranaceous, with caducous cilia, the outer surface sparsely strigose-glabrescent centrally. Flowers 6.7–7.7 by 3.4–4.1 mm; sepals 5, broadly ovate, nearly equal, 3–3.6 by 2.5–3.3 mm (outer), 2.9–3.3 by 2.5–3 mm (inner), sclerotic basally and chartaceous above, the base broadly cordate, the apex rounded, the margin membranaceous, with caducous cilia and dark basal setae (outer sepals) or pale basal flaps (inner sepals), the surfaces glabrous; corolla urceolate, the petals 5, distinct or slightly connate basally, ovate, nearly equal, 5.3–6.4 by 2.1–3.4 mm, membranaceous in lower  $\frac{1}{4}$ – $\frac{1}{3}$ , sclerotic above, the apex obtuse, recurved at anthesis. Staminate flowers with stamens 18, uniseriate, slightly adnate basally, unequal, unordered, filaments flat; long stamens with the filaments linear, ca. 1.8 mm long, the anthers ovate, ca. 1.1 by 0.8 mm, the apiculus ovate, 0.1 mm long, apically rounded; short stamens with the filaments linear or geniculate, 0.9–1.1 mm long, the anthers ovate, 0.7–1 mm long, basally cordate, the apiculus ovate, 0.1–0.2 mm long, apically rounded; gynoecium narrowly conical, the ovary 3-locular, ca. 1.1 by 1.5 mm, with ovules ca. 7 per locule on 2 pendulous axile placentae, the style abruptly tapering to linear, ca. 2.2 mm long, the stigmatic lobes 3, erect, ca. 0.25 mm long, the stigmatic surface adaxial, dark, minutely papillate. Carpellate flowers with



FIGURE 3. a-i, *Freziera minima*: a, habit, from below; b, shoot apex; c, undersurface of leaf; d, flower; e, petal of staminate flower, stamens adnate; f, gynoecium of staminate flower; g, gynoecium and staminodia of carpellate flower; h, seed; i, fruit (a-e from type, g-i from *Holm-Nielsen et al.* 3906). j, *Freziera stuebelii*, undersurface of leaf (from photo of type).

staminodes 18, uniseriate, free (1 adnate to inner petal), linear, flat, equal, ca. 1.5 mm long, apically rounded; gynoecium conical, the ovary 3-locular, ca. 1.3 by 1.7 mm, with ovules 8 to 14 per locule, the style ca. 1.9 mm long, the stigmatic lobes 3, slightly flaring, ca. 0.9 mm long, dark, conspicuously pa-

pillate. Fruits ovoid, 6.8–7.5 by 5.1–5.5 mm, with narrow dark band just below stigmas, 2- or 3-locular, locules splitting out of fruit separately as mericarps; seeds 2 to 8 per locule, irregularly rounded, ca. 1.6 mm long, dark brown.

TYPE. Ecuador, Prov. Loja, Zamora-Chinchiipe border, crest of E cordillera, ca. 13 km E of Loja, cloud forest and stunted crest vegetation, ca. 3°58'S, 79°10'W, 2840 m, 28 Jan. 1985, *J. L. Luteyn & E. Cotton 11288* (bud, ♂ fl—holotype, NY; isotypes, AAU, CAS, GH, MO, QCA (n.v.), U).

ADDITIONAL SPECIMEN EXAMINED. Ecuador, PROV. ZAMORA-CHINCHIPE, road Loja-Zamora, km 14, mountain ridges with elfin forest and open bogs, 4°S, 79°09'W, 2750–2770 m, 19–20 April 1973, *Holm-Nielsen et al. 3906* (bud, ♀ fl, fr; AAU).

*Freziera minima* is characterized by minute, broadly ovate, crenate leaf blades. In appearance the foliage does not resemble that of any previously known *Freziera*. Other species with leaves nearly as small are *F. microphylla* Sandw. (11.5–27.5 by 7.4–14.9 mm) and *F. suberosa* Tul. (10.7–18.6 by 7.5–10.4 mm), both of which are densely sericeous on the twigs and leaf undersurfaces and have revolute and therefore apparently entire leaf margins, quite unlike *F. minima*. Other species such as *F. euryoides* Kobuski and *F. parva* Kobuski, which have relatively small leaves and are sparsely pubescent (like *F. minima*), have leaves two to five times longer than those of *F. minima*. *Freziera minima* may also be closely related to the following species (see below).

***Freziera stuebelii* (Hieron.) A. Weitzman, comb. nov.**

FIGURE 3j.

*Taonabo stuebelii* Hieron. Bot. Jahrb. Syst. **21**: 320. 1896. TYPE: Colombia, Cerro Patascoy, 3300 m, *Stübel Colomb. 366* (holotype, B, destroyed; photos at GH, MO, negative at F (no. 9738)).

*Patascocya stuebelii* (Hieron.) Urban, Ber. Deutsch. Bot. Ges. **14**: 283. 1896.

*Ternstroemia stuebelii* (Hieron.) Kobuski, J. Arnold Arbor. **23**: 343. 1942, as *stuebelii*, nomen illegit.

*Freziera stuebelii* was collected only by Stübel at Cerro Patascoy, Colombia. It is known only from a photograph of the holotype, which was destroyed at Berlin (no isotypes are known). Urban (1896) mentioned the likely relationship of *Patascocya* Urban to *Freziera* because they both have distichous leaves, pubescence, and relatively few stamens. The photograph of the type suggests similarity in habit, at least, to *Freziera*, and the leaves are similar to those of *F. minima*, both having very broadly ovate, crenate blades about 1 cm long and wide. Although no flowers or fruits are visible in the photograph, according to the descriptions provided by Hieronymus (1896), Urban (1896), and Melchior (1925), the flowers agree in all characters with those of *Freziera*.

When placing this species in its own genus, Urban (1896) heavily emphasized the two bractlike structures at the base of the pedicel and the position of the ovules. In both *Freziera minima* and *F. stuebelii* the solitary flowers are subtended by two bractlike structures; these are morphologically similar to the single bracts that subtend each flower in an inflorescence of other species of *Freziera*. The fact that there are two such structures in these species is not surprising since they are the equivalent of bud scales and since branches in

*Freziera* usually are just an extension of the inflorescence axis. In describing *Taonabo stuebelii*, Hieronymus (1896), following Szyszyłowicz's (1893) keys to the Theaceae, placed the species in *Taonabo* Aublet (= *Ternstroemia* Mutis ex L.f.) because that genus has pendulous ovules with apical placentation and *Freziera* has exclusively axile placentation. I have observed pendulous placentae and ovules in several species of *Freziera*. For example, in functionally staminate flowers of *F. minima*, there are ca. seven ovules per locule that hang from two pendulous axile placentae, which may appear apical.

Compared to *Freziera minima*, *F. stuebelii* has leaves that are broader and more cordate at the base, with the lateral veins apparently sunken above, very prominent below, and bifurcate instead of reticulate (compare FIGURE 3c and j). Bifurcate venation is unknown in other species of *Freziera*. All other aspects of leaf morphology are apparently similar to those of *F. minima* and are present elsewhere in the genus. In all species of *Freziera* most small veins that go to the margin end in a seta, as they do in *F. stuebelii*, although in the other species the veins are reticulate.

The relatively slight differences between *Freziera* and *Patascoya* discussed above do not warrant generic status for *Patascoya*. Based on the evidence at hand, I believe that *F. stuebelii* belongs to *Freziera* and is most closely related to *F. minima*.

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